

Synlophe of *Cooperia neitzi* (Trichostrongylidae: Cooperiinae) with Comments on Vulval Inflations and Hypertrophy of Cuticular Ridges among the Trichostrongylids

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ABSTRACT: The synlophe of *Cooperia neitzi* is characterized by a closed pattern in the cervical region (most similar to *C. punctata* and *C. pectinata*), a minuscule lateralmost ridge, 20 ridges at the level of the excretory pore and cervical papillae in males and females, and sequential addition of ridges laterally starting near the midbody (20 and 24 ridges at the midbody of males and females, respectively, with a maximum of approximately 32 adjacent to the copulatory bursa and vulva). The characteristic bilateral vulval fan in females has a consistent structure, being supported by a pair of hypertrophied ridges in each subdorsal field adjacent to the lateralmost ridge. Three species typical of bovids in sub-Saharan Africa (*C. neitzi*, *C. verrucosa*, and *C. okapi*) share the characters of minuscule lateralmost ridges, a closed cervical synlophe, and cuticular inflations at the level of vulva. Comparisons to other species of Cooperiinae (*Parostertagia heterospiculum*, *Cooperia verrucosa*, and *Cooperia okapi*) indicate homology in the bilateral and symmetrical structure of the vulval fans recognized in species of the subfamily. In contrast, it appears that the irregular and asymmetrical cuticular inflations reported or observed at the level of the vulva among certain Ostertagiinae (*Longistrongylus* spp., *Mazamastrongylus* spp., and *Camelostrongylus mentulatus*) have a fundamentally different configuration. It is suggested that vulval inflations in the Cooperiinae and Ostertagiinae had independent origins and thus are convergent.

KEY WORDS: *Cooperia* spp., Cooperiinae, Ostertagiinae, Trichostrongylidae, synlophe, morphology.

Cooperia neitzi Mönnig, 1932, was described from kudu (*Tragelaphus strepsiceros* (Pallas)) in the Transvaal, South Africa (Mönnig, 1932, 1933). Travassos (1937) and Skrjabin et al. (1954) included this species in monographs on the Trichostrongylidae but did not augment the description. Gibbons (1981) provided a redescription of males and females based on material from the type host in Zimbabwe. However, synoptic accounts of the synlophe are lacking, although some aspects including the disposition of ridges ventrally and the form of prominent bilateral inflations at the level of the vulva in females were depicted in the original description by Mönnig (1933), and Gibbons (1981) documented the structure and numbers of ridges near the midbody.

The current study arose from the necessity to understand the structural basis for cuticular inflations in the vulval regions of some species of the Cooperiinae (*Parostertagia heterospiculum* Schwartz and Alicata, 1933; *Cooperia neitzi*; *C. okapi* Leiper, 1935; *C. verrucosa* Mönnig, 1932; and perhaps others) and the Ostertagiinae (species of *Mazamastrongylus* Cameron, 1935, and *Longistrongylus* Le Roux, 1931, and *Camelostrongylus mentulatus* (Railliet and Henry, 1909)) and their relationship to the synlophe (Mönnig,

1933; Gibbons, 1977, 1981; Hoberg and Lichtenfels, 1992; Lichtenfels et al., 1993). Specifically, a requisite for the phylogenetic analysis of the trichostrongylids resides in determining the homology for these and other characters among the 6 subfamilies currently recognized as valid (see Gibbons and Khalil, 1982b; Durette-Desset, 1983; Hoberg and Lichtenfels, 1992).

In the current study we describe the synlophe in males and females of *Cooperia neitzi*. The cervical synlophe is compared among *C. neitzi* and those species of *Cooperia* previously evaluated (Lichtenfels, 1977; Gibbons, 1981). Additionally, observations of the structure of vulval inflations (based on transverse sections near the level of the vulva) including position and relationship to the synlophe are presented for *C. neitzi*, *Mazamastrongylus* sp., *Longistrongylus sabie* (Mönnig, 1932), and *Camelostrongylus mentulatus*. These latter data provide a basis for preliminary comparisons of vulval fans or inflations reported among the Cooperiinae and Ostertagiinae.

Methods and Materials

Nematodes were examined as temporary whole mounts cleared in phenol-alcohol (80 parts melted phenol crystals and 20 parts absolute ethanol). Observa-

tions concentrated on *C. neitzi*, and wholemounts were used to study the configuration of the longitudinal ridges laterally and dorsoventrally in the cervical zone, to determine the extent of the synlophe posteriad in males and females, and to examine the structure of vulval inflations in females. Transverse sections from single specimens of female *C. neitzi*, *C. okapi*, and *Longistrongylus sabie* and from two specimens each of *C. mentulatus* and *Mazamastrongylus* sp. were prepared freehand with a cataract knife and embedded in glycerine jelly. Sections were used to study the structure of the synlophe, with particular reference to the configuration of the vulval inflations characteristic of these species. Line figures and photomicrographs of sections are as viewed from the anterior and oriented with dorsal toward the top of the plates; all line figures were prepared with aid of a camera lucida. Terminology for the structure of the synlophe is consistent with that developed by Lichtenfels (1977) for *Cooperia* spp. The term *cuticular strut* follows Lee (1965).

Specimens examined

Cooperia neitzi: material included 5 female and 3 male specimens from the type host collected in Zimbabwe (listed as Rhodesia) by J. B. Condry and made available from the collection of the International Institute of Parasitology, St. Albans, U.K. (No. 904).

Specimens examined for comparative purposes are the following. *Cooperia okapi*: material included 6 female specimens from *Okapia johnstoni* (Sclater) in Zaire (listed as Epulu, Belgian Congo) and deposited in the U.S. National Parasite Collection, USDA, Beltsville, Maryland (No. 61409). These specimens were originally included in the type series of *Cooperia okapi* van den Berghe and Vuylsteke, 1937, a synonym of *C. okapi* (see van den Berghe and Vuylsteke, 1937). *Cooperia punctata* (von Linstow, 1906) and *C. pectinata* Ransom, 1907: material included 5 male specimens of each species from *Bos taurus* Linnaeus representing unaccessioned material from the U.S. National Parasite Collection. *Longistrongylus sabie*: material included 5 females from *Aepyceros melampus* (Lichtenstein) in Kruger National Park, South Africa, and deposited in the U.S. National Parasite Collection (No. 77484). *Camelostongylus mentulatus*: material included 5 females each from *Camelus* sp. in the U.S. National Zoo and from *Lama glama* (Linnaeus) in Oregon, deposited in the U.S. National Parasite Collection (Nos. 32079 and 82440, respectively). *Mazamastrongylus* spp. (including both *M. odocoilei* (Dikmans, 1931) and *M. pursglovei* (Davidson and Prestwood, 1979)): material included 5 females examined by Lichtenfels et al. (1993) from *Odocoileus virginianus*.

Results

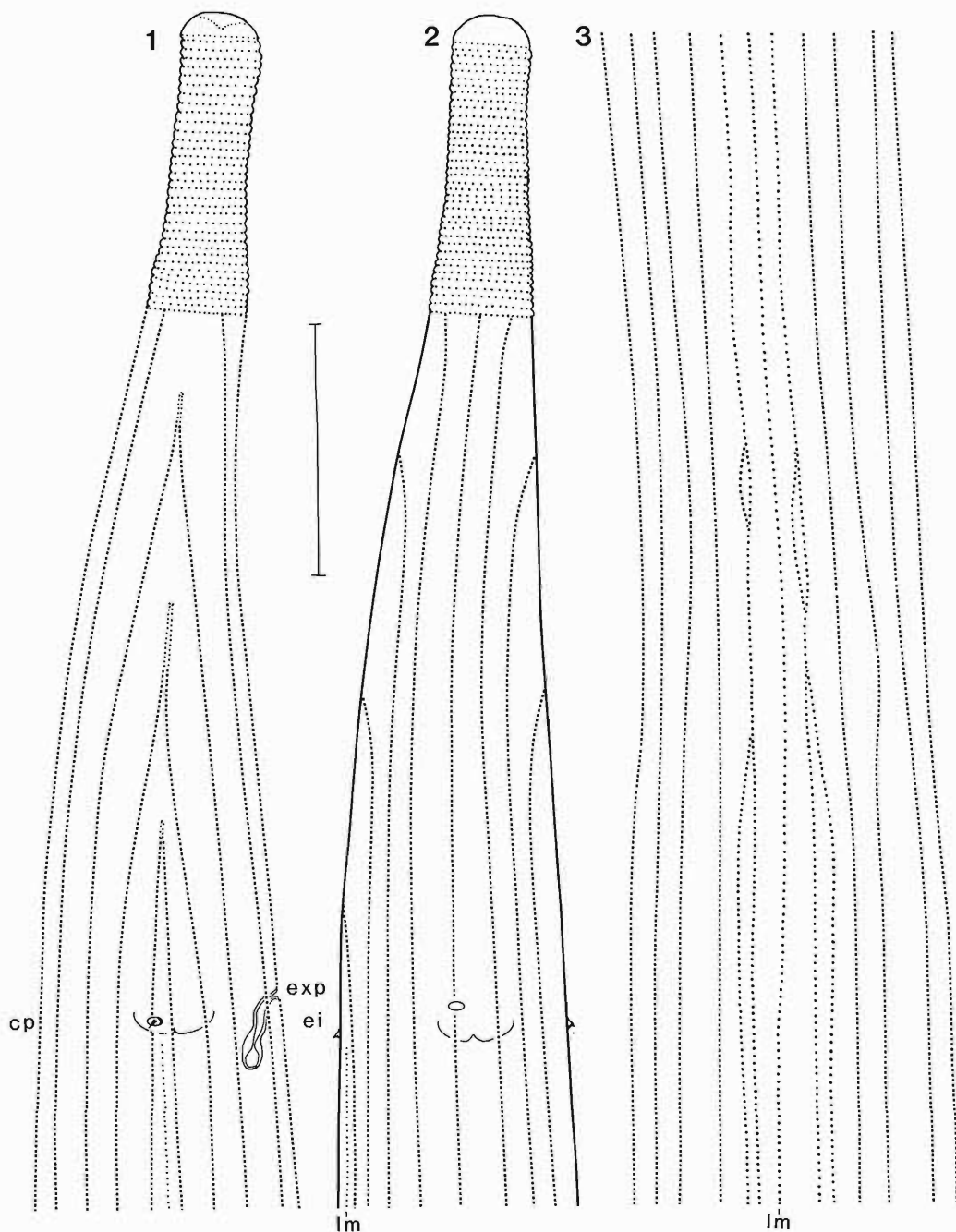
Synlophe of *C. neitzi*

The structure of the synlophe in males and females of *Cooperia neitzi* shares basic similarities. A bilaterally symmetrical system of well-defined ridges extends from the base of the cephalic expansion to the anterior margin of the bursa in males and beyond the anus in females

(Figs. 1–3). The striated or beaded appearance of the synlophe is attributable to the structure of underlying struts supporting individual ridges.

In the cervical zone of males and females (level of excretory pore and base of esophagus), there are 20 ridges (7 ventral and 7 dorsal with broad inter-ridge intervals, and 3 smaller, narrowly spaced ridges in each lateral field) that are continuous and extend into the posterior ¼ of the body to terminate adjacent to the caudal extremity (Figs. 1–3). Those in the lateral field are arranged bordering a minuscule lateralmost ridge (Figs. 1, 3). A closed pattern is typical for 3 pairs of ridges in each lateral field in the cervical zone (Fig. 1). As these pairs converge toward a caretlike point in the anterior, the narrowly spaced ridges become parallel and diminished in height and may continue for 20–30 µm before termination. Ventrally and dorsally, 3 ridges extend to the base of the cephalic expansion, and the ventral ridge is interrupted at the level of the excretory pore (Fig. 2).

Posteriad from the cervical zone, there is a sequential increase in the numbers of ridges beginning near the midbody in females and in the posterior ¼ of the body in males. Addition of new ridges consistently occurs adjacent to the 3-ridge lateral system, with initiation of ridges usually being convergent on the pair that directly borders the minuscule lateralmost ridge (Fig. 3). Anterior to the point of initiation of each new pair of ridges, irregularities develop, with short regions where individual ridges bifurcate and anastomose (Fig. 3). In males there are 20 ridges (7 large dorsal and ventral, 3 small in each lateral field) at the midbody; posteriad there are 6 pairs of ridges that originate laterally in the posterior ¼ of the nematode (originating in 3 consistent zones at approximately 77, 90, and 95% of body length from the anterior) for a maximum of 32 (7 dorsal and ventral, 9 in each lateral field). In females there are 20–25 ridges at the midbody (Fig. 5); posteriad 4–6 pairs of continuous ridges are added in the region from the midbody to anterior to the vulva for a maximum of 32 (attained at 75–80% of body length from the anterior). Only rarely do new lateral ridges originate beyond the 3-ridge lateral system; variation in females is also due to sporadic occurrence of short, discontinuous ridges in the lateral field. All ventral ridges are interrupted at the level of the vulva; the numbers of ridges then increase to approximately 30 posterior to the vulva with irregular loss of lateral ridges occurring in the



Figures 1-3. Drawings of the synophe in female and male specimens of *Cooperia neitzi* (scale bar = 100 μ m). 1. Cervical region of female specimen, lateral view showing typical closed pattern (see Lichtenfels, 1977), and minuscule lateralmost ridge (exp = excretory pore, cp = cervical papilla, ei = esophageal-intestinal junction). 2. Cervical region of female specimen, ventral view showing 3 continuous ventral ridges extending to the base of the cephalic expansion, and minuscule lateralmost ridges (lm). 3. Posterior quarter of a male specimen, lateral view showing typical pattern of addition of ridges in the lateral field. Note minuscule lateralmost ridge (lm) and irregularities in the synophe anterior to the point of origin of new ridges.

region anterior to the anus; posteriad extension of the synlophe occurs beyond the anus.

Bilateral vulval fan in *C. neitzi*

A prominent bilateral inflation, 200–230 μm in length, occurs at the level of the vulva (approximately 80% of the body length from the anterior). The form and orientation of the inflation is consistent in all specimens (Figs. 4, 6, 7). Each fan is formed by the hypertrophy of struts supporting a pair of specific lateral ridges in each subdorsal field (Figs. 4, 6, 7). Origin of the inflation in the subdorsal field adjacent to the minuscule lateralmost ridge is accompanied by hypertrophy of the ridges (Figs. 4, 6), inflation of the cuticle, and substantial disruption of the synlophe with interruption of a number of ridges in the lateral fields, including the lateralmost. At the greatest width of the fans (Figs. 4, 7), near the level of the vulva, considerable curvature is observed as bilaterally the inflations and supporting struts attain a ventrally directed orientation. Posterior to the ovejectors, the structure of the synlophe regains the symmetry and orientation evident in the midbody of the nematode.

Vulval inflations among other species

Transverse sections at the level of the vulva among representatives of the Ostertagiinae revealed cuticular inflations (distinct from vulval flaps) to be variable in extent, generally asymmetrical, and disposed dorsally, laterally, or lateroventrally. Hypertrophied struts do not provide direct support for these irregular inflations.

Ornamentation adjacent to the level of the vulva in *Mazamastrongylus* spp. is relatively complex, and there is no specific orientation or symmetry in the disposition of cuticular inflations. Inflations are highly irregular, being composed of dorsally, ventrally, or laterally directed cuticular crests or broader hypertrophied regions (Figs. 8, 9). One to several ridges of the synlophe (occasional fusion of ridges is observed) may be associated with each inflation. Enlarged struts are absent or poorly defined and only indirectly constitute the foundation for inflated regions (Fig. 9).

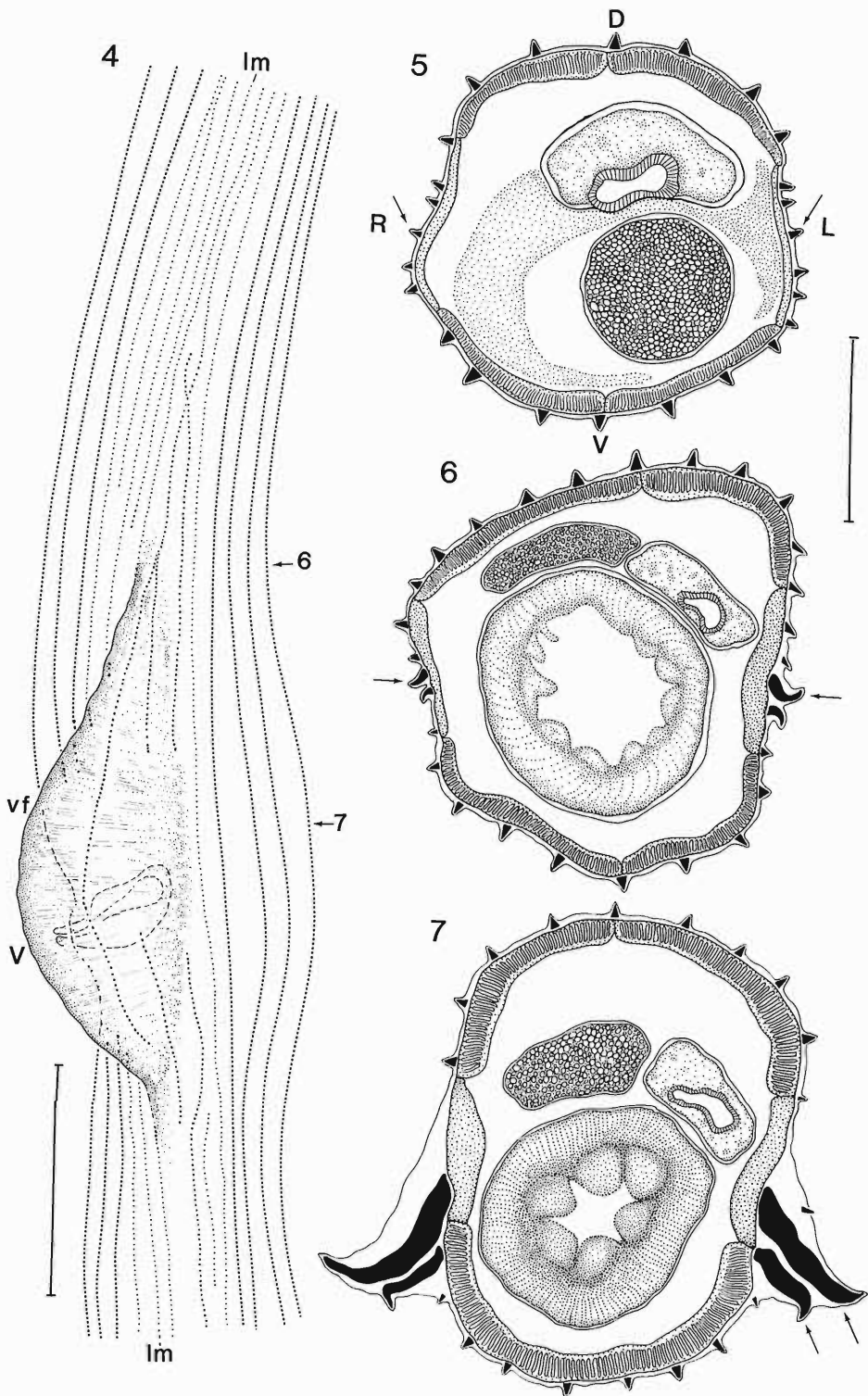
Substantial inflations at the vulva typical of *Longistrongylus sabie* are to some extent bilateral to ventrolateral in disposition. Each major inflation is a multiridge system variable in development, and irregular hypertrophy of adjacent dorsal ridges is also evident (Fig. 10). The synlophe is superficial with respect to the bilateral inflations, and prominent struts providing direct support of hypertrophied regions and ridge systems are absent (Fig. 10).

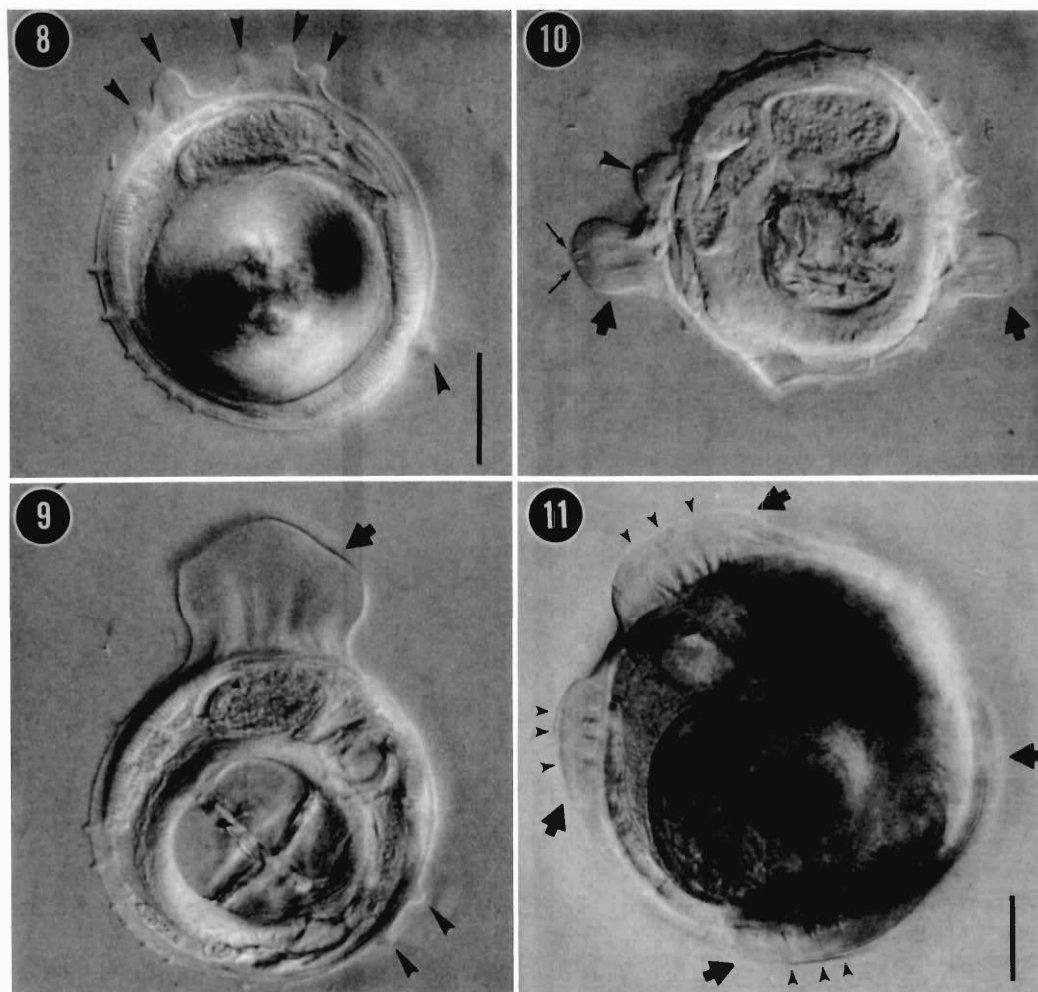
Broad, rounded inflations (1–4 in number) disposed dorsally or laterally are typical of the vulval region in *Camelostrongylus mentulatus* (Fig. 11). Hypertrophied regions of the cuticle and synlophe represent multiridge systems lacking specific orientation or symmetry. Strutlike formations are evident but appear as irregular rod-like structures deep within the inflated cuticle (Fig. 11).

Discussion

The synlophe in males and females of *Cooperia neitzi* has never been completely characterized, nor has the structure of the cervical syn-

Figures 4–7. Synlophe and cuticular fans at the level of the vulva in females of *Cooperia neitzi* (scale bar = 100 μm for Fig. 4; 50 μm for Figs. 5–7). 4. Vulval region in left lateral view showing configuration of the synlophe and origin (in the subdorsal field adjacent to the lateralmost ridge) and structure of the vulval fans (only left lateral fan is depicted). Note that the ridges of the lateral fields are typically smaller than those in the ventral or dorsal fields (lm = lateralmost ridge, v = vulva, vf = vulval fan). The figure is orientated with anterior toward the top; positions of transverse sections depicted in Figures 6 and 7 are indicated by arrows. 5. Synlophe at the midbody (transverse section as viewed from the anterior, with dorsal [D] oriented toward the top, ventral [V] toward bottom, and left [L] and right [R] indicated) showing position of lateralmost ridges (arrows); 25 ridges are present with 7 large ventral and dorsal ridges and 6 and 5 smaller laterals. 6. Synlophe near the point of initiation of the fans showing subdorsal hypertrophied struts and lateral ridges (arrows). There are 29 ridges present with 7 large ventral and dorsal and 7 and 8 laterals. Interruption of the lateralmost has occurred slightly anterior to the position of this section. 7. Synlophe near level of vulva and widest extent of bilateral fans showing massive hypertrophied struts (arrows) supporting the cuticular inflation (directed slightly ventrad); 23 ridges are present with 7 dorsal, 6 ventral, and 6 and 4 laterals. In this section a ventral ridge adjacent to the vulva has been interrupted.





Figures 8–11. Cuticular inflations in females among some species of the Ostertagiinae shown in transverse section near the level of the vulva (scale bars = 25 μ m; same scale for Figs. 8–10). 8. *Mazamastrongylus* sp., sectioned at the level of the anterior sphincter, showing initial development of irregular cuticular crests and hypertrophy of ridges dorsally and lateroventrally (pointers) that constitute the prominent vulval inflations. 9. *Mazamastrongylus* sp., sectioned at the level of the anterior vestibula, showing full extent of a dorsal vulval inflation (arrow), lacking highly distinct supporting struts, that has developed from the fusion of the cuticular crests shown in Figure 8; note hypertrophied ridges in lateroventral field (pointers). 10. *Longistrongylus sabie*, sectioned through the vestibule, showing laterally oriented inflations (large arrows) and hypertrophy of a single laterodorsal ridge (pointer). Note the minuscule struts of two ridges (small arrows) that indicate the synlophe is superficial with respect to the inflations. 11. *Camelostrongylus mentulatus*, sectioned anterior to the vulva, showing 4 rounded cuticular inflations (arrows), with one being beyond the plane of focus. Note the irregular rodlike struts deep within the inflations (pointers).

lophe in any of the species typical of African ruminants been compared in detail to those occurring in North America (Lichtenfels, 1977; Gibbons, 1981). Results of the present study are in general agreement with previous reports but provide additional details of the structure and distribution of longitudinal ridges. Mönnig (1933)

described 20–30 continuous longitudinal striations in males and females and depicted the interruption of the ventral synlophe and the presence of a pair of lateral alae at the level of the vulva in females. Gibbons (1981) found 20 (7 dorsal and ventral, 3 in each lateral field) and 19 ridges, respectively, at the midbody in females

and males but did not evaluate the cervical zone. In the present study we found 20 ridges at the midbody of males and 20–25 in females and a maximum of 30–32 in the posterior $\frac{1}{4}$ of the body. With respect to Gibbons (1981), the discrepancies in the number of midbody ridges relate to variation in the point of origin (near the midbody) for lateral ridges in females and an apparent irregular discontinuity in a left lateral ridge in the male specimen examined in her study (see Fig. 49 of Gibbons, 1981).

The cervical synlophe has been evaluated in detail for 6 species of *Cooperia* from ruminants in North America (Lichtenfels, 1977). The "closed pattern" was designated for 4 species (*C. pectinata*, *C. punctata*, and *C. oncophora* (Railliet, 1898) and *C. surnabada* Antipin, 1931) where pairs of ridges converge symmetrically and terminate laterally in the cervical zone (Lichtenfels, 1977). The pattern apparent in *C. neitzi* is similar to that described for *C. pectinata* and *C. punctata*, except in the former species there are 20 cervical ridges (compared to 14, with 5 large dorsal and ventral ridges and 2 small ridges in each lateral field), 3 pairs converge and terminate laterally (compared to 2 pairs), and a minuscule lateralmost ridge in each lateral field is not evident in the other species (Lichtenfels, 1977). Absence of the lateralmost ridge in *C. pectinata* and *C. punctata* was confirmed by midbody sections depicted by Gibbons (1981).

Variation in the configuration of the closed pattern (structure of the "caretlike" anteriorly directed points where ridges converge and terminate) was evident in a comparison of *C. neitzi* and specimens of *C. punctata* and *C. pectinata* examined during the present study and is greater than that previously documented by Lichtenfels (1977). Specifically, in *C. neitzi* and these other species, ridges converge laterally to form a prominent caretlike point but then may extend parallel (with a very narrow interval separating the ridges) for 20–105 μ m before terminating (Fig. 1). Thus, although the typical closed pattern is evident (in contrast to the "open pattern" typical of *C. curticei* (Railliet, 1893) and *C. spatulata* Baylis, 1938), the anteriorly directed "caret-like points" described by Lichtenfels (1977) are not always sharply delineated. Additionally, in both *C. pectinata* and *C. punctata*, the most anterior pair of ridges (labeled D-1 and V-1 in Fig. 1 by Lichtenfels, 1977) may converge and extend to the base of the cephalic capsule as a single ridge.

Among species of *Cooperia* endemic to Africa

in which the cervical zone has been examined, the closed pattern (consistent with that observed in *C. neitzi*) has been depicted for *C. verrucosa* from *Tragelaphus oryx* (Pallas) (see Gibbons, 1981) and is apparent in *C. okapi* from *Okapia johnstoni* (Hoberg, unpubl. data). These species also possess a single minuscule lateralmost ridge in each lateral field, discernible in whollemounted specimens extending the length of the nematode and also evident in sections at the midbody, similar in form to that described in *C. neitzi* (see Gibbons, 1981). In contrast, *C. rotundispiculum* Gibbons and Khalil, 1980, from *Redunca redunca* (Pallas) is characterized by an open system (similar to that described for *C. curticei*) and lacks a diminutive lateralmost ridge (Lichtenfels, 1977; Gibbons, 1981). Although requiring confirmation, it appears that the diminutive lateralmost ridge may be correlated with the closed pattern of the cervical synlophe and may potentially indicate a more inclusive group of *Cooperia* spp. occurring in bovids endemic to sub-Saharan Africa. This contention is further supported by the presence of 20 midbody ridges (7 large dorsal and ventral, 3 small ridges in each lateral field) in *C. neitzi* and *C. verrucosa*, although the number in *C. okapi* (14–16 in males and females) is more typical of other *Cooperia* spp. (Gibbons, 1981).

Posterior to the cervical zone, Lichtenfels (1977) noted a sequential increase in the numbers of ridges in the lateral fields of the synlophe among the 6 species considered from North America. This pattern of ridge addition (laterally in the posterior) was also observed in the present study and appears to be a uniform character among *C. neitzi*, *C. okapi*, *C. verrucosa*, and other *Cooperia* spp. Addition of new ridges typically occurs adjacent to the pair of ridges that border the lateralmost (or the pair of lateralmost ridges when the minuscule ridge is absent). Ridges are either initiated in the space between ridges (e.g., *C. pectinata*) or appear to originate directly from the edges of the lateral ridges (e.g., *C. neitzi* [Fig. 3], *C. punctata*).

Cuticular inflations or fans at the level of the vulva have been recognized in a number of *Cooperia* spp. but are particularly well developed in *C. neitzi* and *C. verrucosa* and to a lesser extent in *C. okapi* (Mönnig, 1933; Travassos, 1937; Gibbons, 1981; Hoberg and Lichtenfels, 1992). The bilateral fans typical of *C. neitzi* are supported by 2 hypertrophied struts (see Lee, 1965) and represent 2 specific lateral ridges in each

subdorsal field (see Figs. 4, 6, 7). Although the origins of the inflations are in the subdorsal field, at the maximum extent of development there is a ventral orientation for these ridge systems (see Figs. 4, 7). Mönnig (1933) clearly depicted the subdorsal origin of the fans while describing a pair of prominent lateral alae at the level of the vulva (also shown by Travassos, 1937), whereas Gibbons (1981) showed the fans with an origin in the ventrolateral field. Neither of these earlier studies provided a lateral view of the cuticular ridges in the vulval region.

The structure of the fan in *C. verrucosa* is highly similar to that described in the present study for *C. neitzi*. The lateral view of the synlophe in the vulval region of the former species by Mönnig (1933) unequivocally shows the origin of the fan from a single ridge in the subventral field (ventral to the lateralmost ridge). Although it is not evident whether or not more than a single ridge is involved in the structure of each fan, Mönnig (1933) indicated that "... one of the longitudinal striations is raised into an alar expansion. ..." Gibbons (1981) did not evaluate the configuration of the synlophe in the vulval region of *C. verrucosa*.

In contrast to *C. neitzi* and *C. verrucosa*, fans evident in *C. okapi* differ in form (see Gibbons, 1981). In the latter species, all ventral and dorsal ridges become hypertrophied. However, it is specifically the ventrolateral ridges that attain the greatest height and thus form the impression of a small, elongate, bilateral fan at the level of the vulva (Gibbons, 1981; Hoberg, unpubl. obs.). At the level of the vulva, all ridges remain discrete and there are no irregular enlargements (inflations) of the cuticle associated with fusion of individual ridges comprising the synlophe. The ridges ventral in position to the lateral field are consistently the largest. Thus, in these 3 species of *Cooperia*, in which fans are recognized, minuscule lateralmost ridges and a closed pattern in the cervical synlophe are also consistently present (see Gibbons, 1981).

In the Cooperiinae, vulval fans are typically bilateral and symmetrical and appear to arise from specific ventral or dorsal ridges in the lateral fields (intergeneric and interspecific differences are apparent, but intraspecific variation is minimal) (Hoberg and Lichtenfels, 1992). There appears to be a general consistency in the configuration of the fans among the Cooperiinae where this character has been examined (e.g., *Parostertagia heterospiculum*, *C. neitzi*, *C. verrucosa*, and

C. okapi) (Mönnig, 1933; Gibbons, 1981; Hoberg and Lichtenfels, 1992). Other characters largely restricted to the Cooperiinae include a small number of ridges in the synlophe and convergent addition and increase posteriad in the numbers of ridges along with specific attributes of the bursa (Durette-Desset, 1982, 1983; Gibbons and Khalil, 1982b; Hoberg and Lichtenfels, 1992).

Prominent inflations at the level of vulva are relatively rare among the trichostrongylids, being reported only among the Cooperiinae as indicated earlier and among some of the Ostertagiinae (specifically, *Mazamastrongylus* spp., *Longistrongylus* spp., *Cameloststrongylus mentulatus*, and possibly *Cervicaprastrongylus malviyai* (Chaturvedi and Kansal, 1977)) (Gibbons, 1973, 1977; Gibbons and Khalil, 1982a; Lichtenfels et al. 1993; Hoberg, unpubl. data). Inflations and bilateral fans appear distinct from vulval flaps known among the Ostertagiinae, the Haemonchinae, and the Cooperiinae (e.g., structures present in some *Ostertagia* spp., *Haemonchus* spp., and *Paracooperia* spp.) as the latter typically represent a posteriad extension of the body wall that partially or completely envelops the region of the vulva in females (see Skrjabin et al., 1954). In contrast, inflations are hypertrophied regions of the cuticle often intimately associated with the synlophe, as described previously. This distinction is particularly evident among some of the Ostertagiinae, where inflations and vulval flaps may be present concurrently in females of *Mazamastrongylus* spp.

Vulval inflations among the Ostertagiinae appear to be fundamentally different from those characteristic of the Cooperiinae. Whereas bilateral and symmetrical fans are typical of the latter subfamily, irregular inflations associated with the synlophe have been evaluated in *Mazamastrongylus*, *Longistrongylus*, and *Cameloststrongylus* (Gibbons, 1972, 1973, 1977; Lichtenfels et al., 1993) and recently recognized in *Hyoststrongylus rubidus* (Hassall and Stiles, 1892) (Hoberg, unpubl. data; see Hassall and Stiles, 1892; Goodey, 1924). In these genera of the Ostertagiinae, inflations are asymmetrical, irregular systems of multiple or discontinuous ridges disposed dorsally, laterally, and lateroventrally (Figs. 8–11). Fusion of ridges is also often associated with the development of inflations among species of these genera. Additionally, the direct relationship of hypertrophied struts and inflation of the cuticle, established for the Cooperiinae, is

apparently not as well defined among the Osteragiinae (Hoberg and Lichtenfels, 1992). Thus, it is suggested that vulval inflations among the Cooperiinae and Ostertagiinae are convergent. However, among genera and species within each subfamily, characteristic cuticular inflations may represent putative homologies (synapomorphies) indicative of more inclusive relationships. Results of the current study provide additional support for placement of *Parostertagia heterospiculum* in the subfamily Cooperiinae (see Hoberg and Lichtenfels, 1992).

Acknowledgments

We gratefully acknowledge Dr. Lynda Gibbons of the International Institute of Parasitology, St. Albans, U.K., for kindly making specimens of *C. neitzi* available for study. Dr. Lora Rickard, College of Veterinary Medicine, Oregon State University, provided some specimens of *C. mentulatus* from llamas. Mr. Robert Ewing and Mr. Arthur Abrams of the Biosystematic Parasitology Laboratory, completed the final line drawings and assisted in preparation of the descriptions, respectively.

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